

Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*)

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Despite the widespread occurrence of avian duets, their adaptive significance is poorly understood. It is generally assumed that they function in the joint defense of territories, but no study has successfully distinguished between this hypothesis, which invokes cooperation between the sexes, and mate defense, which invokes conflict. Further, most duetting studies have focused on oscine passerines, the songs of which are learnt and relatively complex. We therefore tested the mate defense hypothesis in the warbling antbird (*Hypocnemis cantator*), an Amazonian suboscine that produces simple sex-specific songs and duets. Acoustic analysis of songs showed (1) that solos were often produced by males, but rarely by females; (2) that duets consisted of a male song and a female reply; and (3) that, although female song was invariable, a swift reply resulted in males producing shorter songs with fewer notes. These results suggest that duetting, and the structure of duets, is chiefly a product of female behavior, a scenario more suggestive of conflict than cooperation. To investigate this idea we carried out playback experiments, which showed that (4) the response to solo songs was sex specific (i.e., male solos elicited a strong response from paired males, and female solos elicited a strong response from paired females); (5) males and females responded to same-sex solos more strongly than to duets; and that (6) females answered their partner's songs more often, and more rapidly, in response to female solos than male solos or duets. Although it can be argued that sex-specific responses to solo song result from intrasexual territorial defense, we cannot use the same reasoning to explain (5) or (6). Instead, these observations imply that solitary intruders were more threatening than paired intruders, and thus that the perceived threat was to the partnership rather than the territory. Taken together, findings (1) to (6) suggest that females adjust their vocal behavior in relation to the level of perceived threat to the partnership, and duet with males in order to repel same-sex rivals. This study therefore strengthens support for the mate defense hypothesis, and suggests that conflict—rather than cooperation—may have played a major role in the evolution and maintenance of avian duets. *Key words:* duets, *Hypocnemis cantator*, mate defense, playback experiments, territory defense, warbling antbird. [*Behav Ecol*]

The adaptive significance of coordinated vocal duets is poorly understood, and, until recently, this fascinating form of animal communication was neglected by behavioral ecologists (Hall, 2004; Langmore, 2002). This is despite the fact that duetting occurs in birds at least as often as cooperative breeding and interspecific brood parasitism (i.e., 3% of species), subjects that have been intensively studied for decades (Clutton-Brock, 2003; Davies, 2000).

The past 5 years, however, have seen a resurgence of interest in duetting, with most research indicating that—in support of the traditional stance—duets are primarily used in joint territory defense (Grafe and Bitz, 2004; Grafe et al., 2004; Hall, 2000; Langmore, 1998; Sonnenschein and Reyer, 1983). Several recent studies also found evidence that males and/or females reply to their partner's solo songs either to prevent them from deserting (Appleby et al., 1999; Hall, 2000; Mulder et al., 2003) or to prevent themselves from being usurped by same-sex rivals (Grafe and Bitz, 2004; Seddon et al., 2002), providing at least tentative support for the idea that duets may arise through conflict. However, these studies could not distinguish between cooperation and conflict because the territory and mate defense hypotheses generate similar predictions, that is, that duets are loud, locatable, used in interactions with neighbors, and are incited by playback of

solos and duets, with solos eliciting sex-specific responses (Hall, 2004).

Nonetheless, there are at least two predictions that distinguish these hypotheses. One is that same-sex solos elicit stronger responses than duets or opposite-sex solos because solitary intruders are more threatening than paired intruders, the threat being to the partnership rather than the territory. The second is that paired birds should reply to more of their partner's songs and should do so more promptly after same-sex solos than opposite-sex solos or duets. The logic is that frequent and prompt replies to a partner's songs signal the presence of a well-defended bird that is unavailable for pairing with the intruder.

Only three studies have explicitly tested these predictions, and the support they provide is mixed and to a certain extent limited by small sample sizes. No support was found for the first prediction in the tropical boubou (*Laniarius aethiopicus*) (Grafe and Bitz, 2004) and the Australian magpie-lark (*Grallina cyanoleuca*) (Mulder et al., 2003), and although males (but not females) respond to more of their partner's songs after same-sex solos in the boubou, neither males nor females have been shown to do so in the magpie-lark. Although there is tentative support for both predictions in the subdesert mesite (*Monias benschi*), in this case interpretation is made difficult by the fact that this is a group-living, chorusing species in which the vocal behavior of other group members is probably confounding (Seddon et al., 2002). Thus, there is still uncertainty as to whether duets arise through conflict between the sexes and further experimental tests are required.

Another limitation of previous work is that almost all studies have been carried out on oscine passerines (Hall, 2004). Apart from a single study of dusky antbirds, *Cercomacra tyrannina*,

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carried out more than a decade ago (Morton, 1996; Morton and Derrickson, 1996), scant attention has been paid to the suboscine passerines (suborder Tyranni) of the Neotropics. This is despite the fact that they account for at least 20% (1151 species) of all passerine species (Sibley and Monroe, 1990), and include three extremely diverse families, the tyrant flycatchers (Tyrannidae), the ovenbirds (Furnariidae), and the antbirds (Thamnophilidae). In these New World assemblages duetting is a fairly common behavioral trait (see reviews in del Hoyo et al., 2003), suggesting that studies focusing on suboscines could provide key insights into the evolution and adaptive significance of duetting.

We therefore tested the mate defense hypothesis in the warbling antbird (*Hypocnemis cantator*), a suboscine passerine common and widespread in the understory of the Amazon rainforest. As a territorial and socially monogamous species that produces structurally simple solos and duets, it is ideal for testing ideas about the function of duetting. Moreover, unlike most duetting species studied to date, warbling antbirds have sexually dimorphic plumage, making it possible to quantify male and female behavior in the field without the need for individual marking and post hoc molecular sexing.

Previous studies indicate that male and female warbling antbirds produce sex-specific songs, and that females reply vocally to their partner to produce duets (Isler et al., in press; Zimmer and Isler, 2003). If these arise through conflict, with females duetting to prevent themselves from being usurped by rivals, we make the following predictions (see Table 5): (1) duets are initiated by males, (2) the structure of male but not female song changes during duet formation, (3) males and females respond more strongly to same-sex solos than to opposite-sex solos; (4) males and females respond more strongly to same-sex solos than to duets; and (5) females reply to their partner's songs more often, and more promptly, in response to female solos than to male solos or duets. Predictions (1) and (2) are consistent with mate defense because they suggest that duet formation and the extent of a male's contribution to a duet depends entirely on the behavior of the female. Prediction (3) is equivocal, as sex-specific responses to playback can be explained either by intrasexual territorial aggression or mate defense. However, these hypotheses are distinguished by predictions (4) and

(5), both of which indicate that solitary same-sex intruders are more threatening than opposite-sex or paired intruders, and hence that the threat is to the partnership rather than the territory.

In the first detailed experimental study of duetting in a suboscine bird, we used playback experiments in conjunction with acoustic analyses to test these predictions and found compelling support for the mate defense hypothesis.

METHODS

Study species

The warbling antbird is a medium-sized (11–12 cm, 10–14 g), sexually dimorphic and socially monogamous passerine bird from Amazonian rainforest (Zimmer and Isler, 2003). Pairs maintain year-round territories (Terborgh et al., 1990), and their offspring have low levels of dispersal (Bates, 2000). In common with many antbirds, males and females produce loud vocalizations on a daily basis and throughout the year, consisting of multiple notes delivered in a stereotypic pattern as solos or duets. Because this differs from the traditional, rather narrow definition of song—that is, complex male vocalizations used in mate advertisement (Catchpole and Slater, 1995)—the term “loudsong” has been coined (Willis, 1967; Zimmer and Isler, 2003). Although loudsongs are probably functionally analogous to “songs,” we retain the term loudsong to be consistent with previous work. In this study we use the following definitions.

Loudsong: a more or less discrete unit repeated during a bout of singing. It consists of a stereotypic series of notes in which the interval between successive notes is smaller and more consistent than that occurring between successive loudsongs (Figure 1). In the warbling antbird, male and female loudsongs consist of a series of 6–18 notes descending in both pitch and pace. Male loudsongs have a single introductory note, an even-pitched, even-paced main phrase, and usually terminate in 1–4 low-pitched, slow-paced raspy notes (Figure 1a–c). Female loudsongs have 1–4 introductory notes and an even-paced main phrase that descends slightly in pitch and usually terminates in 1–4 raspy notes (Figure 1d–f).

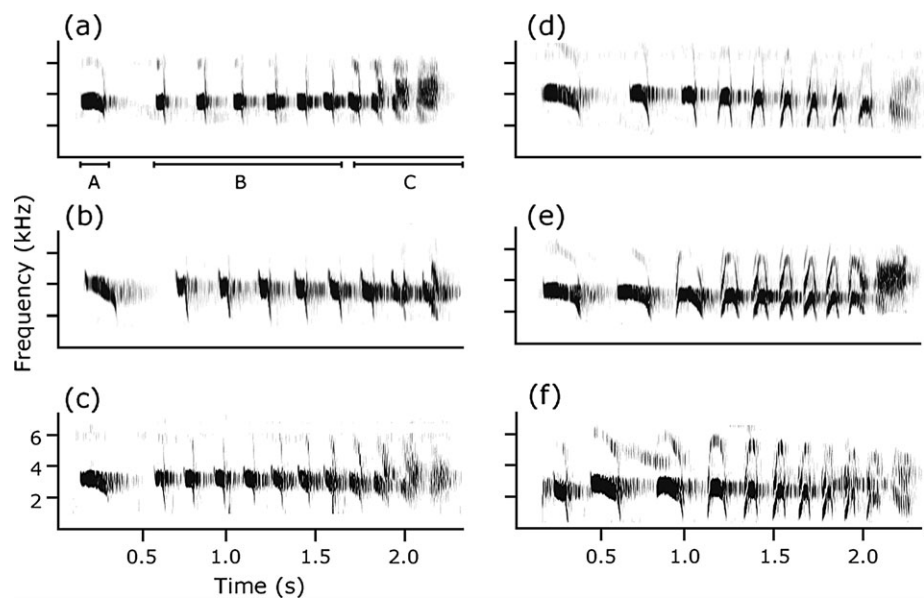


Figure 1
Audiospectrograms of loudsongs of three different males (a–c) and females (d–f), illustrating variation between individuals and between the sexes and showing: A (the introductory note), B (the main phrase), and C (the terminal phrase) of the male loudsong.

Solo: a series of male or female loudsongs.

Duet: a single pair of loudsongs comprising one male and one female loudsong where the interval between male and female loudsongs within a duet is always much shorter than that between successive duets (see Figure 2). For a detailed description of the acoustic properties of warbling antbird vocalizations, see Isler et al. (in press).

Long considered to be a single species, the *Hypocnemis cantator* complex probably contains at least six species-level taxa, each occupying a more or less distinct geographic region within the Amazon basin and foothills of the Andes (Isler et al., in press). According to this recent research, the focus of the present study is the nominate race of *Hypocnemis striata*, the spix's warbling-antbird, a taxon restricted to lowland rainforest south of the Amazon in Brazil. For the purpose of this study, and for the sake of simplicity, we retain the traditional taxonomy.

Study population

In May–July 2004 we studied a total of 22 pairs of warbling antbirds at Rio Cristalino Jungle Lodge, located 40 km north-east of the town of Alta Floresta in Mato Grosso State, south-central Brazil (9° 41' S, 55° 54' W). The site consists of approximately 100 ha of pristine lowland tropical moist forest and is accessed by a grid of trails encompassing the territories of at least 30 pairs of warbling antbirds. For a full description of the site see Zimmer et al. (1997). Although we did not color band individuals, the points at which experiments were carried out and recordings made were marked with coded flagging; no further experiments or recordings were made from the same pair. Warbling antbirds are highly territorial, sedentary, and vocal, and we were able to delimit territories by tracking the movement of singing birds and marking the location of countersinging individuals. Where territory boundaries were less clear, we ignored any male heard singing within 100 m of our flagged locations. Given the small size of known territories, this rule of thumb provided a safeguard against pseudoreplication.

Acoustic analysis of loudsong structure

A Sennheiser ME66-K3U directional gun microphone and a Sony TC-D5 Pro II tape recorder were used to record solos and duets onto 60 min TDK metal tapes. Using Avisoft

SASLabPro Version 4.15 (Raimund Spect, Berlin, Germany) with a 16-bit acquisition sound card (0 VIA [Wave] 5.10), taped loudsongs were automatically filtered at half the Nyquist frequency to prevent aliasing and digitized twice, once at a sampling frequency (SF) of 44.1 kHz and once at a SF of 12 kHz. We obtained 300 min of recordings of solos and duets from a total of 22 males and 16 females. Using only high-quality recordings (i.e., those with low background noise made 5–15 m from singing birds), loudsongs were described quantitatively by taking a variety of temporal and frequency measurements from audiospectrograms using Avisoft's on-screen cursors. To achieve maximum temporal resolution (1.5 ms), time features were taken from audiospectrograms from recordings sampled at 44.1 kHz using the broadband (323 Hz) filter settings (Fast Fourier Transformation = 512, Frame = 50%, Window = FlatTop, Overlap = 88%). To maximize frequency resolution (11 Hz), audiospectrograms were also produced from recordings digitized at 12 kHz using the narrowband (55 kHz) filter settings (FFT = 1024, Frame = 100%, Window = hamming, Overlap = 88%). Loudsong structure was quantified using the following standard time (in seconds) and frequency (in kilohertz) measures (see Figures 1 and 2): (1) total number of notes, (2) number of terminal raspy notes, (3) duration of loudsong (excluding final raspy notes because of uncertainty as to when these notes ended), (4) overall pace (number of notes, excluding terminal raspy notes, divided by loudsong duration), (5) pace of middle phrase (number of notes in middle phrase divided by duration of middle phrase); (6) duration of first note, (7) duration of interval between the first and second note, (8) bandwidth of first note, (9) bandwidth of middle phrase, (10) maximum frequency of loudsong, (11) minimum frequency of loudsong, and (12) bandwidth of loudsong. Frequency measures could not be measured reliably from amplitude spectra because of interference by background noise, especially the songs of other birds and insects.

Playback experiments

Selecting only those recordings made in natural situations, that is, without playback, we viewed broadband audiospectrograms of stimulus loudsongs with Avisoft to ensure that there was no background noise in the frequency range of warbling antbird loudsongs. We then normalized their amplitude and digitally filtered them to remove low- and high-frequency background noise (FIR bandpass filter set between 1 and 8 kHz). Stimulus sound (uncompressed "wav") files 1-min long were then created using Avisoft. Each consisted of the same loudsong repeated every 15 s, matching the natural rate of four loudsongs per minute. These stimulus wav files were then transferred to a minidisk using SonicStage Software Version 1.5 (Sony Corporation, New York, NY).

Playbacks were conducted on a total of 18 pairs from 10 June–5 July 2004 at 0600–1000 h to minimize effects on responses of date and time of day. Experimental subjects and their neighbors were at different stages of their breeding cycle. Because it was not possible to determine stage of breeding cycle of all pairs when carrying out the experiments, we used date of trial instead. Each pair received three playback treatments: male solo (a series of four male loudsongs), female solo (a series of four female loudsongs), and duets (a series of four duets with minimal overlap between male and female loudsongs; e.g., Figure 2a). We used 18 unique sets of solos and duets as stimuli for 18 pairs to avoid pseudoreplication (following Kroodsma, 1989). Treatments were separated by an interval of 48 h to minimize habituation, and each pair received the treatment in a random order. All playbacks were given from the same location and at a similar time

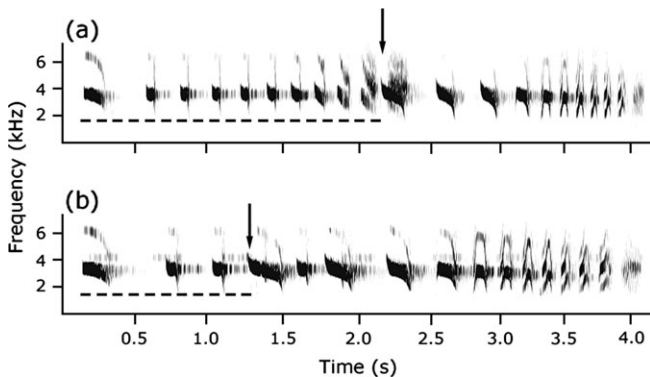


Figure 2
Audiospectrograms of duets given by the same pair of warbling antbirds showing (a) slow and (b) rapid replies by the female to her partner's loudsong. Arrows show the point at which the female starts to sing; dashed lines denote female reply time.

of day (to within 1 h). To avoid the problems of habituation and nonindependence of trials, pairs on adjacent territories were not tested on the same day. Although no evidence of neighbor-stranger recognition was found in the spotted antbird (*Hylophylax naevioides*) (Bard et al., 2002), it does occur in another species of suboscine, the alder flycatcher (*Empidonax alnorum*) (Lovell and Lein, 2004). As recognition of neighbors may have confounded our results, we ensured that all pairs received loudsongs from birds recorded from territories at least three territory diameters away (>500 m).

Each trial lasted 10 min (1 min of playback and 9 min of silence). During the first minute, loudsongs were played through a Sony SRS-58 loudspeaker connected to a Sony Net MD Walkman (MZ-N710). The loudspeaker was placed at least 20 m from a territory boundary, approximately 0.2 m up and facing the subjects, which were always located 15–20 m away. The peak sound pressure level (SPL) was adjusted to approximate that of natural loudsongs, that is, 60 dB SPL at 10 m measured with an Adastra handheld analog sound level meter (set at “C” weighting and fast response). Playback experiments were started once the subjects and their neighbors had been silent for at least 5 min. The timing of trials started at the beginning of the first loudsong of the playback.

Quantifying response to playback

During each 10-min trial, one observer used a tape recorder to record as much of the vocal response as possible, and a second observer used a dictaphone to record the location and behavior of subjects. We noted which sex was the first to vocalize (i.e., give a loudsong or a call) and which was the first to approach (i.e., fly toward) the loudspeaker. Responses of each pair member were further quantified by recording the following continuous measures: (1) time from the start of playback to the first visible flight towards the loudspeaker (approach latency in seconds), (2) closest distance (in meters) to the loudspeaker, (3) maximum song perch height (in meters), (4) time (in seconds) spent <5 m from the loudspeaker, and (5) time from the start of playback to the first loudsong (song latency in seconds). Low values for (1), (2), and (5) and high values for (3) and (4) indicated strong responses. In addition, we recorded whether or not the white interscapular feathering was exposed and whether or not the birds flew around the loudspeaker in short rapid flights; these measures indicated high levels of aggression (Robinson and Terborgh, 1995).

We also used the aforementioned Sennheiser microphone and Sony tape recorder to record any solos and duets given after playback. Where possible, we analyzed at least the first six successive male and female loudsongs or duets given after playback, ignoring the first two, the quality of which was often compromised by the gain adjustments made by the recordist. Using broadband audiospectrograms generated from the recordings as previously described, we measured (1) the proportion of male loudsongs replied to by females and (2) female reply time (i.e., the time elapsing between the start of a male's loudsong and the beginning of his mate's; see Figure 2). When a female was present but did not answer her partner's loudsong, an arbitrary reply time was scored as 1.3 s (i.e., the modal duration of a single male loudsong).

Statistical analyses

In the acoustic analyses, for each pair we calculated a mean value for each time and frequency variable measured from male and female loudsongs and a mean female reply time. We tested whether among-individual and among-sex loudsong differences exceeded within-individual and within-sex differences, using one-way ANOVAs on each of the nine acoustic

measures. We used linear regression to test for the effects of female reply time on the duration and number of notes in male loudsongs. Wilcoxon signed-rank tests were used to examine the effects of duetting on the structure of male loudsongs, but we were unable to carry out an equivalent analysis for females because they rarely produced solos. Many of the acoustic variables were intercorrelated. To investigate the effect of playback on overall loudsong structure, we therefore carried out principal component analysis (PCA) and reduced the separate measures to uncorrelated synthetic variables. This method generated three PCs with eigenvalues greater than 1.0, explaining 79.6% of the variance in the acoustic measures. PC1 and PC3 were strongly correlated with temporal characteristics and PC2 with frequency characteristics (see Appendix). To achieve normality and constant variance required by parametric tests, we square-root transformed two variables (number of notes per loudsong and pace), and log transformed all others, prior to carrying out the forgoing analyses.

For the experiments, we first describe the response of pair members to different playback treatments by calculating mean values for the continuous variables (1)–(5). When there was no approach and/or no vocal response, latency to approach and latency to first loudsong was scored as 601 s. Because the response variables were correlated, we performed a PCA to produce a composite measure of response strength. This generated one PC (PC1) explaining 53.9% of the variance in the response variables (eigenvalue = 2.16). PC1 was strongly correlated with approach latency (factor loading = 0.855), closest distance (0.826), maximum height (−0.738), and song latency (0.446). Thus, high values for PC1 indicated a weak response to playback. Linear regression was used to determine if date or time of day had significant effects on PC1. We compared response variables and PC scores for each individual and for each sex using repeated-measures general linear models (GLMs) with playback treatment as the between-subject variable. To examine whether there was a difference between the sexes in the overall strength of response to playback, the male and female scores for PC1 were pooled and sex was defined as the between-subject factor. All response variables apart from one (time <5 min) met normality and equality of variance assumptions after transformation and could be used in the PCA and GLM. Each series of loudsongs and/or duets recorded after playback generated a mean value for female reply time but one absolute value for proportion of male loudsongs replied to by females. Because females often did not sing after male solo playback and because some pairs did not sing after certain treatments, matched data were not available on the effects of playback on the latter two variables. They were therefore compared using Kruskal-Wallis tests. Friedman, Cochran *Q* tests, and repeated-measures GLMs were followed by post hoc multiple comparison tests to examine differences between pairs of treatment on behavior. The determination of significance for these tests was based on an alpha level of .02 (Bonferroni corrected *p* value for three comparisons). Experiment-wide error rates were adjusted with sequential Bonferroni tests (Rice, 1989). Exact *p* values are given where $n < 15$; otherwise asymptotic *p* values are given. All *p* values are two tailed and corrected for ties where appropriate. All statistical tests were carried out using SPSS version 11.01 (SPSS, 1999).

RESULTS

Loudsong and duet structure

Analyzing a total of 278 loudsongs from 22 different males (12.6 ± 5.4 loudsongs per male) and 124 loudsongs from

Table 1
Differences between solos and duets in the structure of the loudsongs of male warbling antbirds

Acoustic measure	Male loudsong		Statistics	
	Solo	Duet	<i>z</i>	<i>p</i>
Total number of notes	12.2 ± 1.3	9.3 ± 1.3	-3.52	<.0001
Number of terminal raspy notes	4.2 ± 0.9	2.0 ± 0.5	-3.52	<.0001
Loudsong duration	1.3 ± 0.14	1.24 ± 0.11	-3.35	.001
Pace of notes in loudsong	9.2 ± 7.5	7.5 ± 0.2	-3.52	<.0001
Pace of notes in middle phrase	10.0 ± 1.6	9.6 ± 1.6	-1.24	.215
Duration of first note	0.14 ± 0.02	0.14 ± 0.02	-0.909	.363
Duration of first interval	0.24 ± 0.02	0.24 ± 0.03	-0.517	.605
Bandwidth of first note	0.64 ± 0.17	0.60 ± 0.16	-0.724	.469
Bandwidth of middle phrase	0.48 ± 0.19	0.37 ± 0.11	-1.81	.07
Maximum frequency of loudsong	3.10 ± 0.19	3.08 ± 0.14	-1.81	.07
Minimum frequency of loudsong	2.62 ± 0.21	2.71 ± 0.15	-2.019	.044
Bandwidth of loudsong	0.48 ± 0.15	0.39 ± 0.12	-2.792	.026

Time variables are given in seconds and frequency variables in kilohertz. Statistics are from Wilcoxon signed-rank tests; *n* = 16 males.

Significant values are denoted in boldface.

16 different females (7.8 ± 3.5 loudsongs per female), we found that male and female loudsongs were individually distinct and sex specific. That is, for all loudsong characteristics measured, variation between individuals exceeded that within individuals in both males (one-way ANOVA: $F_{21,256} > 3.98$, $p < .0001$) and females ($F_{15,102} > 4.81$, $p < .0001$). Similarly, for all loudsong characteristics, except duration, between-sex variation exceeded within-sex variation (duration: $F_{1,401} = 1.35$, $p = .247$; all other characters: $F_{1,401} > 12.5$, $p < .0001$).

A total of 114 duets were recorded from 16 pairs; all were initiated by males. Females rarely produced loudsongs in isolation from their partners: only eight (6% of the total recorded) did not immediately follow male loudsongs. The time taken for a female to reply to her partner's loudsong

varied from 0.45 to 1.77 s (mean ± SD = 0.95 ± 0.30 s, *n* = 114), and female reply time predicted variation in male loudsong duration (linear regression: $F_{1,112} = 41.2$, $r^2 = .27$, $p < .0001$) and note number ($F_{1,112} = 234$, $r^2 = .68$, $p < .0001$). In other words, the more rapidly a female replied to her partner's loudsong, the fewer notes he sang. This suggests that males stop singing when their partners start, an idea corroborated by visual inspection of audiospectrograms. These showed that when females did not reply to their partner's loudsong (e.g., Figures 1a–c) or when they were slow to do so (e.g., Figure 2a), males usually produced a series of terminal raspy notes that are given at a slower pace, lower pitch, and encompass a broader range of frequencies than the notes in the rest of the loudsong. However, when females replied

Table 2
Comparisons within and between the sexes in the response of warbling antbirds to playback of solos and duets, as quantified by three binary variables

Response	Playback treatment			<i>Q</i>	<i>p</i>	Post hoc tests		
	Male solo	Female solo	Duet			MF	MD	FD
Number of occasions when								
♂ initiated vocal response	18	8	15	14.4	.001	NS	NS	NS
♀ initiated vocal response	0	7	2	9.75	.008	*	NS	NS
χ^2_1	18	0.07	9.94					
<i>p</i>	<.001	NS	<.01					
♂ approached first	17	2	10	21.1	<.0001	**	NS	NS
♀ approached first	0	14	3	23.3	<.0001	**	NS	**
χ^2_1	17	9	3.77					
<i>p</i>	<.001	<.01	NST					
♂ gave rapid flights + exposed white mantle	12	2	6	12.7	.002	**	NS	NS
♀ gave rapid flights + exposed white mantle	0	7	1	10.8	.005	**	NS	NS
χ^2_1	12	2.78	3.57					
<i>p</i>	<.001	NS	NS					

Values for chi square and associated *p* derive from chi-square tests; values for *Q* and associated *p* derive from Cochran *Q* tests. Asterisks denote significant differences after Bonferroni adjustment between pairs of treatments using McNemar tests: MF (male versus female solo), MD (male solo versus duet), and FD (female solo versus duet). NS, nonsignificant; NST denotes a nonsignificant trend ($p < .1$).

* $p < .02$, ** $p < .01$.

Table 3
Comparisons within the sexes in the response of warbling antbirds to playback of solos and duets, as quantified by six continuous variables

Response variable	Playback treatment			Statistics		Post hoc tests ^a		
	Male solo	Female solo	Duet	$F_{2,34}$	p	MF	MD	FD
Male ($n = 18$)								
Approach latency	17.6 ± 12.5 (2–50)	49.7 ± 35.4 (10–120)	108 ± 183 (10–601)	12.7	<.0001	.0001	.002	1
Closest distance	2.8 ± 3.4 (0–10)	5.1 ± 2.5 (1–10)	6.7 ± 5.5 (0–20)	11.3	<.0001	.005	.007	1
Maximum height	3.9 ± 1.3 (3–7)	2.7 ± 1.4 (1–7)	3.7 ± 1.4 (2–9)	8.09	.001	.007	.593	.043
Time <5 m	112 ± 98 (0–330)	104 ± 94 (0–330)	117 ± 154 (0–601)	1.2	.549	—	—	—
Song latency	148 ± 82 (40–354)	164 ± 204 (30–601)	160 ± 140 (20–540)	0.62	.546	—	—	—
PCI	−0.99 ± 0.84 (−2.15 to 0.14)	0.12 ± 0.61 (−1.01 to 1.02)	−0.03 ± 0.76 (−1.55 to 1.47)	14.7	<.0001	.0001	.003	1
				$F_{2,26}$	p			
Female ($n = 14$)								
Approach latency	270 ± 265 (3–601)	34.1 ± 37.6 (5–120)	138 ± 200 (10–601)	9.53	.001	.009	.256	.023
Closest distance	11.1 ± 7.6 (1–25)	3.9 ± 2.6 (1–10)	7.6 ± 5.6 (3–20)	5.59	.01	.024	NS	.118
Maximum height	1.9 ± 1.0 (1–4)	3.9 ± 1.3 (2–7)	3.1 ± 1.6 (1–7)	11.3	<.0001	.002	.044	.216
Time <5 m	30 ± 80 (0–300)	118 ± 69 (0–180)	76 ± 102 (0–601)	7.9	.022	<.05	NS	<.1
Song latency	340 ± 220 (70–601)	168 ± 190 (35–601)	307 ± 220 (81–601)	4.49	.021	.019	1	.1
PCI	1.17 ± 1.04 (−0.46 to 2.47)	−0.45 ± 0.55 (−1.08 to 0.94)	0.44 ± 0.82 (−0.61 to 1.66)	12	<.0001	.002	.17	.015

Values are mean ± SD (range). Time variables are given in seconds and distance and height variables in meters. Statistics derives from repeated-measure GLMs, except for variable “time <5 m” for which Friedman tests were used. Significant probabilities after Bonferroni corrections are denoted in boldface ($p < .02$).

^a Post hoc multiple comparison tests examining pairwise differences: MF (male versus female solo), MD (male solo versus duet), and FD (female solo versus duet).

rapidly, fewer terminal raspy notes, if any, were given (e.g., Figure 2b). Perhaps not surprisingly, therefore, we found that the overall structure of male loudsongs differed significantly between solos and duets: compared to loudsongs given as solos, those given as duets were shorter, comprised fewer notes uttered at a slower pace, had a higher minimum frequency, and encompassed a narrower bandwidth (Table 1). Interestingly, however, the acoustic properties of the introductory note and main phrase of male loudsongs did not differ between solos and duets.

Effects of playback on the behavior of males and females

Males responded by singing and/or approaching the loudspeaker in 96% (52/54) of playbacks and females in 72% (39/54; Table 2). Both sexes were more likely to approach and perform rapid flights around the loudspeaker after playback of same-sex solos than opposite-sex solos (all p values < .01; Table 2). Females (but not males) were also more likely to initiate a vocal response after same-sex than opposite-sex solos (p < .02) and were more likely to approach same-sex solos than duets (p < .01). In addition, males were more likely than females to be the first to vocalize, approach and fly around the loudspeaker aggressively in response to male solos (all p values < .001), and be the first to vocalize in response to duets (p < .01). Finally, although males and females were equally likely to be the first to vocalize after female solos, females were more likely than males to approach (p < .01; Table 2).

There was also strong significant variation across playback treatments in three out of the five response variables for males and all five for females and in the principal component scores (PC1) for both sexes (Table 3). Males responded more strongly, approaching more quickly and closely, to male solos than to either female solos (p < .0001) or duets (p = .003; Figure 3a) and also sang from a more elevated perch after male solos than after female solos (p = .007; Table 3). Females, on the other hand, responded much more strongly to female solos than to either male solos (p = .002) or duets (p = .015; Figure 3b), approaching more rapidly and using a higher song perch after female solos than after male solos (p < .01), and approaching more rapidly after female solos than after duets (p = .023; Table 3). Neither sex varied their response between opposite-sex solos and duets. Interestingly, there was a strong effect of sex on PC1 (repeated-measures GLM: $F_{1,30} = 17.3$, p < .0001), indicating that, overall, males responded to playback more strongly than females. Note that there were no significant effects of time of day or date on response to playback as measured by PC1 for males (linear regression: time of day: $r^2 = .041$, $p = .140$; date: $r^2 = .001$, $p = .799$) or females (time of day: $r^2 = .001$, $p = .868$; date: $r^2 = .021$, $p = .362$).

In summary, we found strong sex-specific effects of playback, with males and females responding much more strongly to same-sex solos than to opposite-sex solos or duets.

Effects of playback on the structure of loudsongs and duets

There was significant variation across playback treatment in the acoustic structure of male loudsongs as described by separate measure and principal component scores (Table 4). Compared to loudsongs given after playback of duets, those given after female solos consisted of fewer notes (both total number of notes and number of terminal raspy notes) and were uttered at a slower pace (all p values < .01; Table 4). In addition, loudsongs given after female solos contained fewer notes than those given after male solos (p < .02). Conversely, there were no effects of treatment on the

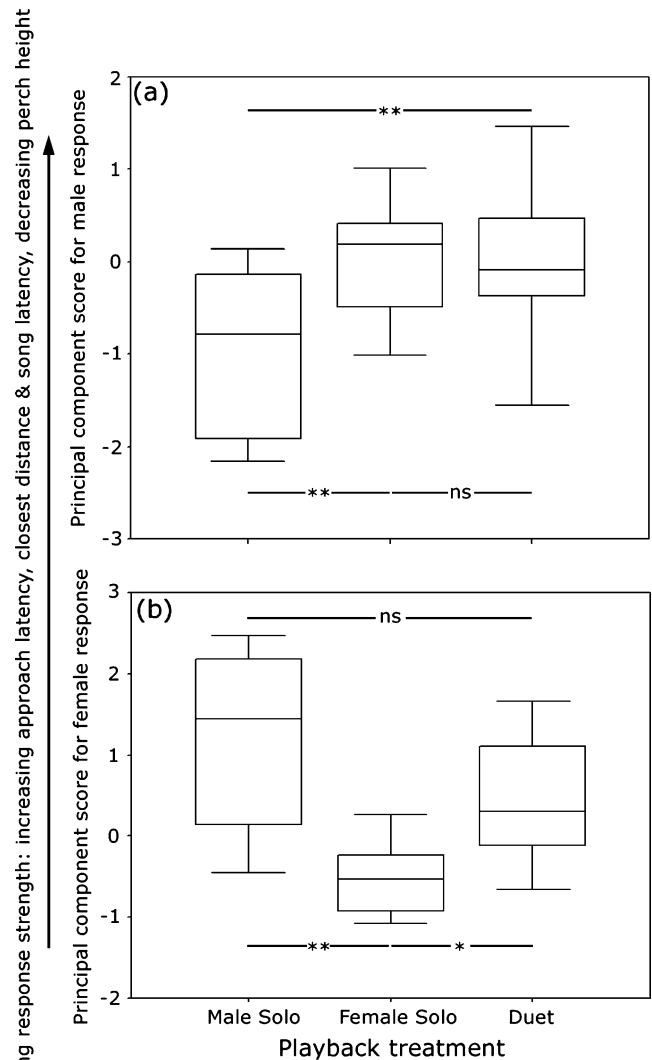


Figure 3

Box plots showing the overall strength of (a) male and (b) female responses to different playback treatments as described by the first principal component (PC1). Boxes indicate the 25th and 75th percentiles, the line in the box marks the median, and the whiskers denote 10th and 90th percentiles. Extreme values are also indicated. Asterisks denote the significance of post hoc multiple comparison tests between pairs of treatments (** p < .01, *** p < .0001).

structure of female loudsongs (p values ranged from .575 to .938).

When analyzing the effects of playback on duetting behavior, we found strong significant variation between treatments in the proportion of male loudsongs answered by females (Kruskal-Wallis test: $\chi^2_2 = 18.4$, p < .0001, $n_{1,3} = 11$, $n_2 = 13$) as well as in the speed with which they replied ($\chi^2_2 = 10.9$, $p = .004$, $n_1 = 9$, $n_2 = 13$, $n_3 = 11$). Females answered a higher proportion of their partner's loudsongs after female solos than after either male solos (p < .0001) or duets (p < .02; Figure 4a), and replied more promptly after female solos than after male solos (p < .001; Figure 4b). Finally, although females answered a higher proportion of their partner's loudsongs after duets than male solos (p < .02), the speed with

Table 4
Effects of playback treatment on the structure of the loudsongs of male warbling antbirds

Acoustic measure	Playback treatment			Friedman tests		Post hoc tests		
	Male solo	Female solo	Duet	χ^2_2	<i>p</i>	MF	MD	FD
Total number of notes	11.6 ± 1.8	10.7 ± 1.9	12.3 ± 2.1	8.4	.008	NS	NS	**
Number of terminal notes	3.5 ± 1.0	2.6 ± 1.3	3.9 ± 1.2	8.4	.008	*	NS	**
Loudsong duration	1.34 ± 0.14	1.30 ± 0.12	1.4 ± 0.2	0.4	.954	—	—	—
Overall pace of loudsong	8.7 ± 1.2	8.1 ± 1.0	8.9 ± 1.3	7.7	.019	NS	NS	**
Pace of middle phrase	10.2 ± 2.2	10.6 ± 2.1	11.8 ± 3.5	1.6	.522	—	—	—
Duration of first note	0.14 ± 0.01	0.14 ± 0.02	0.14 ± 0.02	6.4	.039	NS	NS	NS
Duration of first interval	0.23 ± 0.02	0.24 ± 0.01	0.24 ± 0.02	1.6	.522	—	—	—
Bandwidth of first note	0.56 ± 0.03	0.56 ± 0.08	0.63 ± 0.13	1.3	.549	—	—	—
Bandwidth of middle phrase	0.35 ± 0.09	0.27 ± 0.04	0.40 ± 0.15	5.2	.074	—	—	—
Maximum frequency	3.24 ± 0.14	3.15 ± 0.15	3.11 ± 0.19	0.4	.819	—	—	—
Minimum frequency	2.80 ± 0.26	2.86 ± 0.18	2.66 ± 0.22	4.8	.124	—	—	—
Bandwidth	0.38 ± 0.12	0.33 ± 0.10	0.45 ± 0.13	4.8	.124	—	—	—
PC1	−0.08 ± 0.38	−0.87 ± 0.49	0.31 ± 0.47	8.4	.008	NS	NS	*
PC2	−0.17 ± 0.96	−0.39 ± 0.95	−0.22 ± 1.17	2.8	.367	—	—	—
PC3	−0.07 ± 0.29	−0.05 ± 0.85	0.45 ± 1.51	1.6	.522	—	—	—

Time variables are given in seconds and frequency variables in kilohertz ($n = 6$ males). Significant probabilities are denoted in boldface. Post hoc pairwise tests with Bonferroni adjustments ($p\alpha < .02$) showing effects of treatments on male loudsong structure: MF (male versus female solo), MD (male solo versus duet), and FD (female solo versus duet). NS, nonsignificant.

* $p < .02$, ** $p < .01$.

which they replied did not differ between these two treatments. To those females that were present but did not reply to their partner's loudsong, we gave an arbitrary reply time equivalent to the modal duration of male loudsongs (1.3 s), rather than maximum duration of male loudsongs (1.9 s). We did this so as not to exaggerate the difference between response types, although, if anything, this errs on the side of caution as some responsive females sang toward the end of long male loudsongs. When maximum duration (1.9 s) is used as an arbitrary reply time, not only is the overall effect of treatment on reply time more strongly significant ($\chi^2_2 = 16.5$, $p < .0001$), but female replies to male loudsongs are given significantly more rapidly after female solos than after duets ($p < .02$).

DISCUSSION

Several of the key predictions of the mate defense hypothesis were met in this study, including two that distinguish mate defense from joint territory defense (Table 5). Our results are thereby consistent with the idea that duets in warbling antbirds arise through conflict between the sexes, with females responding to male loudsongs to prevent themselves from being usurped from the partnership.

First we showed that, in common with many other duetting species (Hall, 2000; Hall, 2004), male and female warbling antbirds produce sex-specific songs which are given as either solos or loosely coordinated duets. The sex-specificity of loudsongs is unlikely to be a correlate of sexual dimorphism because males and females are only dimorphic in terms of plumage and not body mass, bill size, or bill shape (Zimmer and Isler, 2003; Seddon N and Tobias J, unpublished data). The implication is that loudsong differences are driven by sexual selection acting directly on the communication system itself.

We found that males initiate almost all duets, that females rarely sing in isolation from males, and that duets therefore occur as a result of females replying to male loudsongs. In this respect, the warbling antbird is similar to the Eastern whipbird (*Psophodes olivaceus*) (Watson, 1969) and the white-browed robin-chat (*Cossypha heuglini*) (Todt et al., 1981) but different

from most other duetting species studied so far in which duets are initiated by females and rely on male behavior (Langmore, 1998, 2002).

Changes in the acoustic structure of the initiator's song during duet formation have been shown in subsdesert mesites, Australian magpie-larks, and Canada geese (*Branta canadensis*) (Hall, 2001; Seddon, 2002; Whitford, 1996) and have been cited as evidence that duets depend on the behavior of both sexes (Seddon, 2002). However, several lines of evidence indicate that male warbling antbirds simply stop singing when females start. First, there was a strong inverse relationship between the speed of a female's reply and the number of notes in her partner's loudsong. In other words, by replying promptly, a female effectively reduced the extent of her mate's vocal signal. Second, males produced a series of slow-paced, low-pitched terminal raspy notes when singing alone, a feature that was omitted or reduced when singing in concert with a female. Third, although the overall structure of male loudsongs differed between solos and duets, the differences could be largely explained by a reduction in the number of terminal raspy notes. And fourth, the lack of significant differences between solos and duets in the acoustic properties of the introductory note and main phrase refutes the idea that females respond to acoustic differences in male loudsong structure. Together these findings suggest that, overall, (1) duet formation mainly depends on female behavior, and (2) females may be able to control the extent of their partner's vocal signal.

Apart from implying that females play an integral role, this suggests that duetting in the warbling antbird is underpinned by a degree of conflict, itself reflected in sexually dimorphic songs and sex-specific responses to playback. These features are common to several other duetting species (reviewed in Hall, 2004) and have been cited as evidence that duets are the by-product of independent territory defense (Morton, 1996; Morton and Derrickson, 1996). This would not explain, however, why duets—including those of the warbling antbird—tend to be more or less coordinated, nor why there is always one sex that waits until the other sex has started singing, even when defending against a same-sex intruder.

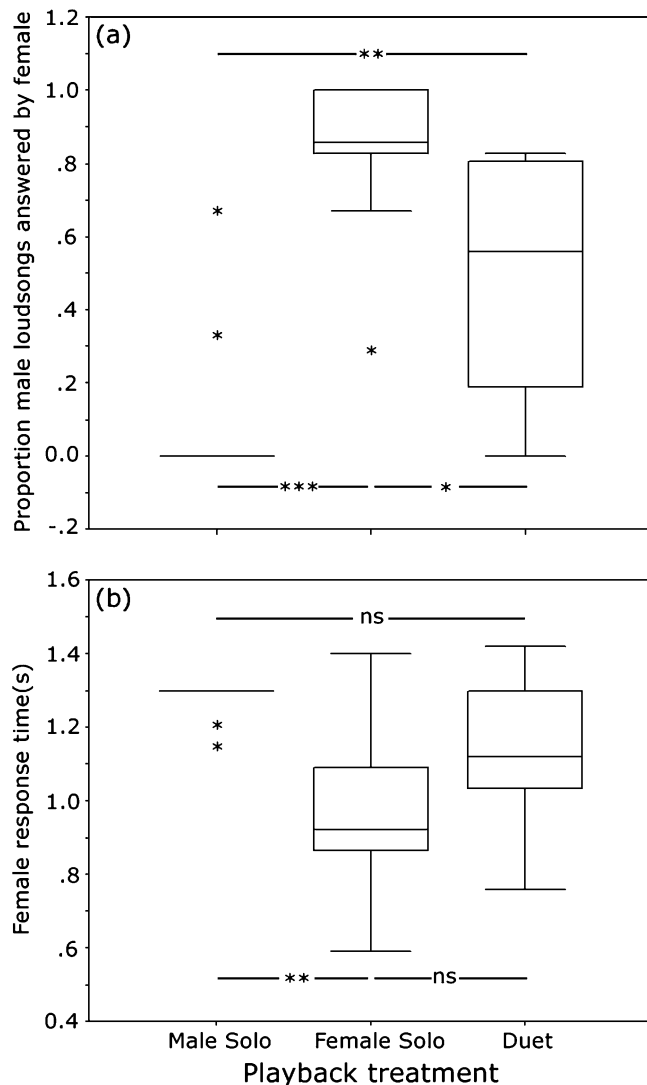


Figure 4
Box plots showing variation between the three playback treatments in (a) the proportion of male loudsongs answered by females and (b) the speed of female responses to partner loudsongs. See Figure 3 for box plot details. Asterisks denote the significance of post hoc multiple comparison tests between pairs of treatments (* $p < .02$, ** $p < .001$, *** $p < .0001$).

We are left with two main alternative explanations for duetting in warbling antbirds, the joint territory defense hypothesis, and the mate defense hypothesis. The loud and locatable nature of warbling antbird duets and the observations that they are used in interactions with neighbors and are readily incited by playback, all suggest that they function in joint territory defense. However, an important prediction of the mate defense hypothesis, and one that clearly distinguishes it from territory defense, is that duets repel unpaired birds. Although the scarcity of unpaired birds in our population meant that it was not possible to test this directly, we nonetheless found support for a related prediction, namely that duets elicit much weaker responses from paired birds than same-sex solos. Indeed, we found that, although not uniformly the case, males and females responded to duets with less vigor than they did to same-sex solos. As highlighted previously, there are two possible alternative interpretations of such a finding (Seddon et al., 2002). One is that by signaling the presence of a pair of intruders, a duet is more intimidating than a solo and therefore

elicits a more cautious response. However, this is refuted by our finding that, overall, paired birds responded to opposite-sex solos and duets with equal strength. The second interpretation is that predicted by the mate defense hypothesis, that is, duets represent less intimidating signals than solos. The logic is that if a duet advertises the intrusion of a mated pair then the threat is to the pair's resources and is thus a territorial issue deserving a unified response, rather than a more direct and insidious threat to the partnership. Our results are consistent with this latter scenario.

Also in support of the idea that duets are a form of mate defense was the finding that, overall, females replied to more of their partner's loudsongs and did so more promptly after playback of female solos than after male solos or duets. Moreover, in replying rapidly, a female shortened her mate's loudsong: male loudsongs comprised fewer terminal notes after playback of female solos than after male solos or duets. In other words, in response to the simulated presence of a same-sex rival on territory, females may be able to reduce the amount of signal produced by their mate by giving prompt replies to his loudsongs. It could be argued that rapid female replies are simply the product of strong intrasexual territorial aggression. However, this does not explain why a female always waits until her partner sings before she does so herself. The most parsimonious explanation is acoustic mate defense.

Apart from mate defense and territory defense, there are two other important hypotheses regarding the primary function of avian duets; one is that they prevent a partner from being usurped, and the other is that they signal commitment (Hall, 2004). We did not explicitly test these predictions because anecdotal observations suggested that they were not relevant to the warbling antbird. Duets are unlikely to prevent a partner from being usurped as this predicts that solos of the opposite sex should increase the likelihood of duetting with a partner (Appleby et al., 1999; Hall, 2000; Mulder et al., 2003), yet in response to male solos, female antbirds rarely sang at all. Similarly, although duetting in some species might discourage desertion because it represents time-consuming, pair-specific investment and thereby signals commitment (Wickler, 1980), this is unlikely to be true in the warbling antbird whose duets are structurally very simple and presumably unlearned, given that song-learning is not thought to occur in suboscines (Kroodsmma, 1996). Moreover, playback experiments in conjunction with temporary removals have shown that, in common with other avian duetters (e.g., tropical boubou; Grafe and Bitz, 2004), females readily perform duets with new and artificial partners (Seddon N and Tobias J, unpublished data); time-consuming investment is clearly not required.

Clearly, duets may serve a variety of secondary functions (e.g., maintenance of contact and synchronization of reproductive physiology; see Hall, 2004), but one primary function in the warbling antbird is the acoustic defense of males by females. In other words, the evolution of duets in this species has been driven, at least in part, by conflict between the sexes rather than cooperation over territory defense, and this is possibly true of other duetting species. That such a conclusion is drawn from work on antbirds might seem surprising given the existence of long-term pair bonds and permanent territoriality in this family (Zimmer and Isler, 2003). Indeed, it is widely assumed that conflicts of interest between the sexes are lower in most tropical passerines than their temperate counterparts (Morton, 1996; Stutchbury and Morton, 2001). However, the fact that the warbling antbird is sexually dimorphic in both plumage and song implies that sexual selection has played a role in the evolutionary history of this species, if not its current mating system. Further work is needed to investigate the intensity of sexual selection in a variety of

Table 5
Predictions of female mate defense hypothesis of duet function and whether they are met in the warbling antbird

Variable	Prediction	Prediction met in present study?
Duet structure	Comprise sex-specific songs	Yes
	Initiated by males (i.e., duets depends on behavior of female)	Yes
	Structure of male but not female song changes in duets	Yes
	Fast replies by females reduces extent of male song	Yes
Response to solos	Attract unpaired birds of the same sex	?
	Elicit strong response from paired birds of same sex	Yes
Response to duets	Repel unpaired birds of either sex ^a	?
	Elicit weak response of paired birds of either sex ^a	Yes
Effect of playback on duet structure	Females reply to more of their partner's songs and do so more promptly after female solos than males solos or duets ^a	Yes

^a Predictions that distinguish mate defense from territory defense.

duetting subsong bird species, perhaps using levels of extra-pair paternity as a measure of conflict between the sexes, and to relate this to patterns of vocal behavior.

In summary, we show that female warbling antbirds reply to their partner's solos to ward off rivals, perhaps by advertising the mated status of the pair, and we thereby provide compelling support for the idea that avian duets are used in mate defense. Moreover, our observation that females might control how much their partners sing is an intriguing possibility that warrants further study.

APPENDIX

Factor loadings on the first three principal components for the nine acoustic measurements taken from the loudsongs of male warbling antbirds

	Factor loadings		
	PC1	PC2	PC3
% of variance	38.7	25.1	15.8
Eigenvalue	3.10	2.01	1.26
Factor loadings			
Total number of notes	0.915	-0.344	0.141
Number of terminal raspy notes	0.885	-0.331	-0.202
Loudsong duration	0.451	-0.192	0.692
Overall pace	0.841	-0.286	-0.343
Pace of middle phrase	—	—	—
Duration of first note	0.060	0.031	0.766
Duration of first interval	—	—	—
Bandwidth of first note	0.206	0.669	0.073
Bandwidth of middle phrase	0.499	0.774	-0.101
Maximum frequency of loudsong	—	—	—
Minimum frequency of loudsong	—	—	—
Bandwidth of loudsong	0.521	0.785	0.029

Loadings $r > |.04|$ are shown in boldface. Emdashes (—) are given for variables that could not be included in the PCA because they violated parametric assumptions.

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REFERENCES

- Appleby BM, Yamaguchi N, Johnson PJ, MacDonald DW, 1999. Sex specific territorial responses in tawny owls *Strix aluco*. *Ibis* 141:91–99.
- Bard SC, Hau M, Wikelski M, Wingfield JC, 2002. Vocal distinctiveness and response to conspecific playback in the spotted antbird, a Neotropical subsongbird. *Condor* 104:387–394.
- Bates JM, 2000. Allozymic genetic structure and natural habitat fragmentation: data for five species of Amazonian forest birds. *Condor* 102:770–783.
- Catchpole CK, Slater PJB, 1995. Bird song: biological themes and variations. Cambridge: Cambridge University Press.
- Clutton-Brock TH, 2003. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–75.
- Davies NB, 2000. Cuckoos, cowbirds and other cheats. London: Poyser.
- del Hoyo J, Elliott A, Christie D, 2003. Handbook of birds of the world, vol. 8, v. 8. Barcelona: Lynx Edicions.
- Grafe TU, Bitz JH, 2004. Functions of duetting in the tropical boubou, *Laniarius aethiopicus*: territorial defence and mutual mate guarding. *Anim Behav* 68:193–201.
- Grafe TU, Bitz JH, Wink M, 2004. Song repertoire and duetting behaviour of the tropical boubou, *Laniarius aethiopicus*. *Anim Behav* 68:181–191.
- Hall ML, 2000. The function of duetting in magpie-larks: conflict, cooperation, or commitment? *Anim Behav* 60:667–677.
- Hall ML, 2001. Duetting and parental care in Australian magpie larks. Canberra: Australian National University.
- Hall ML, 2004. A review of hypotheses for the functions of avian duetting. *Behav Ecol Sociobiol* 55:415–430.
- Isler ML, Isler PR, Whitney BM, in press. Species limits in antbirds (Thamnophilidae): the *Hypocnemis cantator* complex. *Auk*.
- Kroodsma DE, 1989. Suggested experimental designs for song playbacks. *Anim Behav* 37:600–609.
- Kroodsma DE, 1996. Ecology of passerine song development. In: Ecology and evolution of acoustic communication in birds (Kroodsma DE, Miller EH, eds). Ithaca, New York: Cornell University Press; 3–19.
- Langmore NE, 1998. Functions of duet and solo songs of female birds. *Trends Ecol Evol* 13:136–140.
- Langmore NE, 2002. Vocal duetting: definitions, discoveries and directions. *Trends Ecol Evol* 17:451–452.
- Lovell SF, Lein MR, 2004. Neighbor-stranger discrimination by song in a subsongbird, the alder flycatcher, *Empidonax alnorum*. *Behav Ecol* 15:799–804.
- Morton ES, 1996. A comparison of vocal behaviour among tropical and temperate passerine birds. In: Ecology and evolution of acoustic communication in birds (Kroodsma DE, Miller EH, eds). Ithaca: Cornell University Press; 258–268.
- Morton ES, Derrickson KC, 1996. Song ranging by the dusky antbird *Cercomacra tyrannina*. *Behav Ecol Sociobiol* 39:195–201.
- Mulder RA, Bishop H, Cooper M, Dennis S, Koetsveld M, Marshall J, Saunders BL, 2003. Alternate functions for duet and solo songs in magpie-larks, *Grallina cyanoleuca*. *Aust J Zool* 51:25–30.

- Rice WR, 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Robinson SK, Terborgh J, 1995. Interspecific aggression and habitat selection by Amazonian birds. *J Anim Ecol* 64:1–11.
- Seddon N, 2002. The structure, context and possible function of solos, duets and choruses in the subdesert mesite (*Monias benschi*). *Behaviour* 139:645–676.
- Seddon N, Butchart SHM, Odling-Smee L, 2002. Duetting in the subdesert mesite (*Monias benschi*): evidence for acoustic mate-defence? *Behav Ecol Sociobiol* 51:7–16.
- Sibley CG, Monroe BL, 1990. Distribution and taxonomy of birds of the world. New Haven, Connecticut: Yale University Press.
- Sonnenschein E, Reyer H-U, 1983. Mate guarding and other functions of antiphonal duets in the slate-coloured boubou (*Laniarius funebris*). *Z Tierpsychol* 63:112–140.
- SPSS, 1999. SPSS base for Windows user's guide. Version 11.01. Chicago, Illinois: SPSS Inc.
- Stutchbury BJM, Morton ES, 2001. Behavioral ecology of tropical birds. San Diego: Academic Press.
- Terborgh J, Robinson TA, Parker TA III, Munn CA, Pierpont N, 1990. Structure and organisation of an Amazonian forest bird community. *Ecol Monogr* 60:213–238.
- Todt D, Hultch H, Duvall FP, 1981. Behavioural significance and social function of vocal and non-vocal displays in the monogamous duet-singer *Cossypha heuglini* H. *Zool Beitr* 27: 421–448.
- Watson M, 1969. Significance of antiphonal song in the Eastern whipbird, *Psophodes olivaceus*. *Behaviour* 35:157–178.
- Whitford PC, 1996. Temporal alteration and coordination of calls by paired Canada geese in duetted calling of aggression, territorial and triumph behavior. *Passenger Pigeon* 58: 249–258.
- Wickler W, 1980. Vocal duetting and the pair bond. I. Coyness and partner commitment. A hypothesis. *Z Tierpsychol* 52: 201–209.
- Willis EO, 1967. The behaviour of bicolored antbirds. *Univ Calif Publ Zool* 79.
- Zimmer KJ, Isler ML, 2003. Family Thamnophilidae (typical antbirds). In: *Handbook of birds of the world*, vol. 8 (del Hoyo J, Elliott A, Christie D, eds). Barcelona: Lynx Editions, 448–681.
- Zimmer KJ, Parker TA III, Isler ML, Isler PR, 1997. Survey of a southern Amazonia avifauna: the Alta Floresta Region, Mato Grosso, Brazil. *Ornithol Monogr* 48:887–918.